

23.

Display, Breeding and Relationships of Fiddler Crabs (*Brachyura*, Genus *Uca*) in the Northeastern United States.¹

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(Text-figure 1).

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INTRODUCTION.

During the spring and summer of 1943, observations were made near New York City on the display and breeding season of two fiddler crabs, *Uca pugnax* and *U. pugilator*. A few similar notes were taken on the third local fiddler, *U. minax*, during 1941. The purpose of the study was to determine whether these northern fiddler crabs have specifically distinct displays such as were found (Crane, 1941, 1943) to be characteristic of tropical American species during the breeding season, and to see if these displays shed light on the phylogeny of the group.

Previous observers, especially Pearse (1914), Swartz and Safrir (1915) and Gray (1942) in their excellent papers all observed waving in these northern species, but none reported any difference in the procedure of the several species. Pearse alone thought waving to be definitely concerned in courtship, at least to the extent of attracting the attention of the female, and not only as a defense of territory and as a threat to other males. But even Pearse concluded, after remarking that *pugnax* prefers muddy, *pugilator* sandy, locations, "Aside from these differences in habitat and the fact that *U. pugnax* bred earlier in the season than *U. pugilator*, no difference was noticed in the behavior of the two species."

That differences do exist became clearly evident to me during the past summer,

thanks entirely to previous experience in the tropics. Many of the southern species, studied on expeditions of the Department of Tropical Research under the direction of Dr. William Beebe, are more strikingly distinct in their displays than the northern forms, and so, logically, it was they which gave the key to display characteristics. Nevertheless, once the principle of specific behavior variation was understood, the differences between the displays of northern species were obvious at first glance. Finally, prolonged watching proved that without question, waving is an integral part of courtship, just as in tropical fiddlers.

In the present paper, displays and colors will be described in detail under specific headings, along with supplementary taxonomic characters, in order to make the work comparable with the tropical American *Uca* reports. General remarks on breeding season, display and unsolved problems are placed in the concluding section. The usual methods of study were employed: that is, the same beach or mud-flat was used as an observation post as often as possible, and binoculars were found to be invaluable.

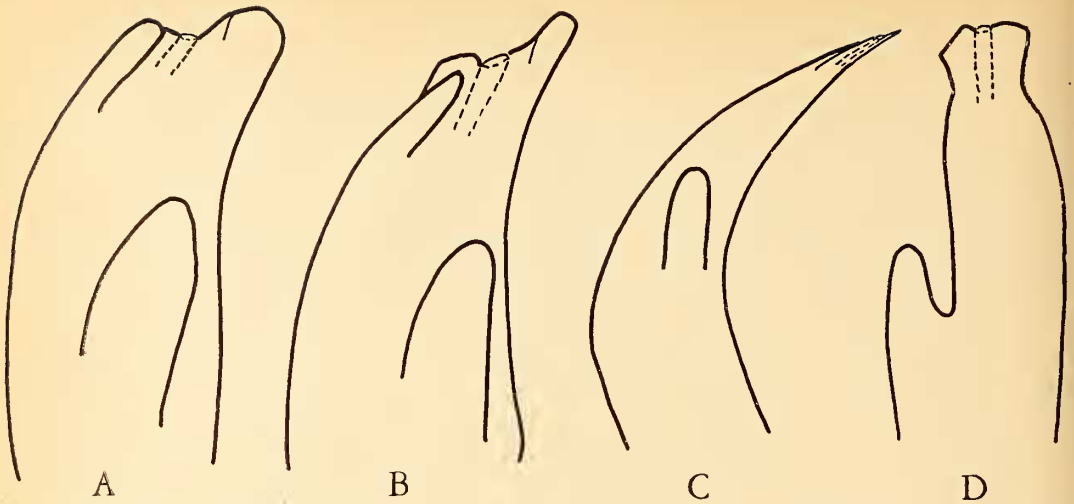
The localities visited included Greenwich, Connecticut; Pelham Bay Park, Port Jefferson and Staten Island, New York; and Atlantic City and Quinton, New Jersey. My appreciation goes to Dr. and Mrs. Robert Cushman Murphy and to Mr. George Agnew Chamberlain for their hospitality during the study of these crabs.

Uca pugnax (Smith, 1870).

(Text-fig. 1a)

References: Gelasimus pugnax Smith, 1870, p. 131; pl. 2, fig. 1.*Uca pugnax*, Rathbun, 1918, p. 395; pl. 139.*Range: From Cape Cod, Massachusetts, to Louisiana.*

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TEXT-FIG. 1. Tips of right abdominal appendages of adult males in *Uca*. **A**, *pugnax pugnax*, anterior view; **B**, *minax*, anterior view; **C**, *pugilator*, anterior view; **D**, same, lateral view. Hairs omitted.

Supplementary Specific Characters: A typical Group 2² *Uca*, in supplementary characters like *pugnax rapax* (Crane, 1943, p. 40), except as follows: there are fewer spoon-tipped hairs on merus of second maxilliped, usually between 10 and 20, rarely up to 25, instead of usually between 70 and 120, rarely as few as 25. Even the tips of the abdominal appendages are practically indistinguishable from those of the subspecies; female always with a well developed genital tubercle.

Color: Displaying males: Carapace dark brown, sometimes grayish or whitish at least on branchial regions in large specimens. Major cheliped outside and in dull brown or brownish-yellow, rarely (outside only) dull apricot yellow, with fingers or entire manus and chelae cream; manus sometimes creamy yellow; eyestalks, top of third maxillipeds and/or front bright turquoise blue (previously unrecorded); minor manus and chelae creamy yellow, sometimes greenish yellow, or even blue-green, almost as bright as the eyestalks. In this species there is relatively very slight brightening of color before display, compared with many tropical forms, or even with *pugilator*. Females scarcely or not at all mottled, dark, with chelae and mani like those of males.

Display: The display of *pugnax*, although obviously related to that of the southern *pugnax rapax*, differs from the latter to a much greater degree than would be suggested by the purely structural differences between the subspecies. Both are slow, as compared with more marine forms, but whereas strong jerking is marked in *pugnax*

rapax, it is indicated only very slightly in *pugnax*, while, on the other hand, a characteristic bobbing curtsy often begins or ends a *pugnax* display, which is never found in the southern form. Also, the display is more variable and sporadic than in *pugnax rapax*. Details are as follows:

The display starts with body elevated only moderately high, both chelae held well off ground and flexed in front of mouth. Major cheliped is unflexed obliquely upward with scarcely the faintest trace of jerking which might be unnoticeable except in view of knowledge of related forms in which jerking occurs. The minor is unflexed simultaneously. Usually with no pause at the peak, the major is brought down into position with something resembling a jerk, or more often several jerklets, as if let down in worn notches so that it slides down with the least hint of "braking." It is only in the most active displays that there is a hint of the pause at the top so characteristic of *pugnax rapax*. During display, as usual in the jerking Group 2 crabs, one or two ambulatories may be lifted and kicked outward at the peak of display. Several steps to one side are often taken on the down stroke. Chelae are usually held almost closed throughout, but sometimes open at the peak of display and sometimes are held open throughout.

At the beginning, or more often, at the end of a display, or sometimes without any waving whatever, a characteristic bobbing, or series of "curtsys" may occur, especially in crabs displaying directly to, or noticed by, a female. It does not precede fights between males, as far as I can see, any more

² For group characteristics, see Crane, 1941, p. 165.

than waving is speeded up before these encounters. This curtsy is not found in any of the other species which I have hitherto observed. It is so fast and slight a motion that it is difficult to analyze, but repeated observation shows the details to be as follows: the body is lowered, with both chelipeds flexed, and simultaneously a double, triple or quadruple tattoo is made with the ambulatories of both sides against the ground. Usually the two middle legs of each side seem to be the ones involved, and their action is frequently alternating.

A second specialization of display, even more climactic in character, was seen once, when the male had attracted a female's attention and had paused halfway down his hole for a final gesture. This took the form of a rigid extension of all the free appendages—major cheliped and four ambulatories—accompanied by a momentary strong vibration of them all. Exactly the same behavior was noted in *saltitanta* under similar conditions, except that in the latter species the cheliped was not involved (Crane, 1941, pp. 154, 191). In *pugnax*, the female did not follow, and the male soon reemerged.

It is impossible to time *pugnax* displays accurately, since they are so variable. However, the average, fast, complete display exclusive of curtsy lasts about 2 seconds.

Rudimentary Shelter-building: In *pugnax* there is evidence that the habit of shelter-building is present in its most elementary form. As in other builders, it occurs in some but not all individual adult, or nearly adult, males. Perhaps the ancestors of the species built always in banks, and the oblique angle of the burrows plus the plugging-up instinct combined to make a pushed-up archway over the door a natural result. This, however, does not explain its absence in the burrows of females. In a colony in relatively sandy soil, mixed with *pugilator*, at Port Jefferson, this habit was first noticed and was more striking than elsewhere: *pugnax* always chose the side of any surface irregularity, for the hole entrance, in preference to flat ground, and there was always in these cases a definite, overhanging hood, though small and poorly formed. This hood I have several times seen shored up with material brought from two or more inches away, just as in the case of true shelter-builders (e. g., *minax*, *cumulanta*, *beebei*, etc.). There is no trace of this behavior in *pugilator*, and the burrow entrances are always in flat areas.

Posing: In *pugnax* the usual brachyuran threat posture of standing motionless with both chelipeds spread wide was observed a number of times, but as Pearse noticed, it had, in this species, nothing apparent to do with fear or threat, either to rival males or

potential enemies. Females were seen to pose also, but not so often, and the majority of posers appeared to be immature. Often one or more ambulatories were kept elevated during posing; usually the crabs faced away from the sun, and remained out of their holes so long that they became quite light gray, apparently from dryness. Often a small elevation was chosen. Every little while they moved slightly, flexing chelae or shifting legs, but not changing ground. They seemed to a certain extent to go into a sort of trance, since they dodged and retreated less than the others when mildly disturbed—say, by a passing car—although when seriously startled, as by the observer's sudden motion, they reached their holes almost as quickly as the others. Sometimes, judging from Pearse's observations, this posing is certainly a part of courtship display, as in some of the tropical species, but at other times it as surely is not. It remains, with shelter-building, one of the mysteries.

Hibernation: On March 15 and 16, colonies of hibernating *pugnax* were examined near Atlantic City, New Jersey, in the salt marshes beside the causeway to Brigantine. The air temperature ranged from 35° to 42° Fahrenheit. The crabs were found, not on the open, spartina-grown flats, but in the foot-high, muddy banks of small creeks, near their mouths, where they opened into sandy-bottomed inlets. They could only have been submerged at occasional spring tides; and the open, weathered, half-frozen burrows, with no traces of tracks or feeding pellets, indicated both that they had not been covered at all and that the crabs had not been active for months. Probably the first activity was just occurring. I saw one female inside the mouth of her burrow, with her eyestalks elevated, although she was incapable of further movement.

The rest of the crabs were all between one and four inches below the surface, the burrows being dug obliquely into the banks, with some individuals lying almost exposed. With the least warming in the hands, or in a jar in the sun, the crabs became active enough to walk fairly rapidly, the young ones warming up first. Crabs were equally divided between the sexes, and were of all sizes, from early post-megalopal stages to large males. They were scattered without arrangement in reference to age or sex, with the young ones often among the deepest, since they had used the holes of large crabs. In the most populous spot, in a section measuring six by six by four inches (144 cubic inches), there were 11 crabs (four young, five adult females, two large males).

It is interesting to compare the shallow excavations of these crabs with Gray's report (1942) that the much larger *minax* hibernates below the frost line. Probably the

latter species, which is often found in almost fresh water, is more subject to freezing and is also less hardy than *pugnax*, which lives in strongly brackish districts.

Uca minax (LeConte, 1855).

(Text-fig. 1b).

References: *Gelasimus minax* LeConte, 1855, p. 403.

Uca minax, Rathbun, 1918, p. 389; pl. 137.

Range: Massachusetts to Texas. Colombia.

Supplementary Specific Characters: A typical Group 2 *Uca*, more closely related to *pugnax* than to *mordax*. Like *pugnax*, in supplementary characters (p. 218) except as follows: spoon-tipped hairs of merus of second maxilliped with spoons exceedingly slender, apparently never more than 10 in number, well developed spoons even fewer; central groove of ischium of third maxilliped exceptionally shallow and slender, curving basally to meet inner groove; gape in minor cheliped sometimes extending only to distal part of serrations; female always with large genital tubercle; tip of abdominal appendage of male as in figure.

Color: (Not observed in bright sunlight, so omitted here; for general color notes, consult Gray, 1942).

Display: The following notes were made on a single, very dark day (July 4), and are not regarded as more than a partial description. Crab rears back on last two or three ambulatories so that carapace is vertical. Major cheliped extended diagonally up, to about half maximum stretch. This position may be held for minutes. In apparently full display, the cheliped is further extended diagonally up to maximum stretch, swiftly, without jerking, then brought down to half-way point or a little below, but not to flexed resting position, in three to five (usually four) decided jerks. Meanwhile the minor chelae perform similar but often completely unsynchronized motions (that is, often the major is going up as the minor comes down). Sometimes the middle ambulatories are elevated during display, as in others of the group. Movement is slow—that is, the jerking portion alone may take two or three seconds.

Uca pugilator (Bosc, 1801-2).

(Text-fig. 1c, d).

References: *Ocypoda pugilator* Bosc, 1801-1802, p. 197.

Uca pugilator, Rathbun, 1918, p. 400; pl. 141; pl. 160, fig. 2.

Range: Massachusetts to Texas; Haiti.

Supplementary Specific Characters: Apparently basically related both to Group 4 (in display and minor cheliped) and Group

5 (in spoon-tipped hairs and abdominal appendage of male). Spoon-tipped hairs on merus of second maxilliped numerous, strongly developed; sometimes as many as 200 may project beyond inner margin of merus, with half as many more non-projecting short ones; in other individuals there is a total of only about 150, arranged in about 10 rows on inner third of merus throughout up to four-fifths of its length. Ischium of third maxilliped with central groove broad, shallow, parallel to inner groove, dying out at beginning of posterior half. Minor chelae with a few strong, jagged, median teeth, and very narrow gape. Sub-orbital region short, triangular, naked except near anterior margin. Abdominal appendage of male with well developed arm (see figure). Female without genital tubercle.

Color: Males, in full display: Carapace creamy white, entire cheliped buffy to creamy white, with base of fingers apricot; at other times, merus is yellowish or apricot. Manus and chelae of minor cheliped also creamy white. Eystalks and ambulatories usually slightly darker, dirty white or buffy, as are underparts, except third maxilliped. Merus of ambulatories on anterior side likely to be darkest. Adult females almost or quite as light as displaying males. Just before assumption of this lightest phase, both sexes usually go through a stage showing a bright purple spot in middle of cardiac region.

Display: Much faster and more energetic than that of *pugnax*, except when the latter is extremely excited: *pugilator* in full display habitually waves at the rate of slightly more than one to the second. The crab starts with body elevated, meral-carpal joint of major cheliped elevated, the chelae tips obliquely lowered, touching ground; cheliped is then raised obliquely up and out, crab stretching meanwhile to extreme tip-toe. The ambulatories, unlike those of *pugnax* and others, are not elevated nor kicked outward at all, except for a rare, obviously accidental elevation of a leg with an especially high stretch. The cheliped is held a fraction of a second at peak, then returned to position, without ever a trace of jerking either on way up or way down. When the crab is greatly excited, the cheliped is not lowered quite to ground after display, nor does he sink so low on the ambulatories; likewise, there is no pause in the rest position, so that the accent comes at elevation of cheliped. Four or five of these peak displays follow each other in a series. Minor cheliped makes weak corresponding gesture. Both pairs of chelae remain practically closed throughout. The crab often remains in one spot, more rarely moves several steps to the side.

TABLE I.

	<i>pugnax</i>	<i>pugilator</i>
Woods Hole, Mass. (Pearse)	July 4-15	First part Aug.
Woods Hole, Mass. (Bumpus)	—	Early June.
Cold Spring Harbor, N. Y. (Swartz & Safir)	At height in mid-Aug.	July 6 to early Aug.

The above is the usual display, but there is an additional sequence reserved for specially excited crabs, often when the female has been attracted to the hole of a male, just before he descends. At full breeding season, it occurs far more often, and sometimes without the noticeable stimulus of a female, than earlier. This excited behavior superficially resembles the curtsy of *pugnax*, but is completely distinct in the means by which it is brought about: It is a rapping gesture made by a tattoo of the flexed cheliped against the ground, as is found in Group 4 crabs, including *cumulanta* and *oerstedii* and culminating in *saltitanta*. The ambulatory take no part in the rapping, and in its less complete stages it is only a quivering of the cheliped.

Another courting behavior sequence was noticed several times in this species, exactly as in *cumulanta* in Venezuela under similar conditions. A male, having attracted a female's attention enough to stop her somewhere near his hole, dodged down into it after frantic waving in the usual way. Also as usual, the female did not follow, but simply remained motionless where she was. Whereupon the male emerged and rushed several inches or more away from the hole on the opposite side from the female, mounted a tiny elevation, and displayed again vigorously, once or twice. Then, holding his cheliped high in the air, he raced again for the hole (toward her), bobbing

somewhat up and down, and vanished after rapping at the mouth of the hole. Once I saw this procedure followed by the prompt approach of the female, who thrust the legs of one side briefly down the hole, but then wandered off. The male emerged and repeated the same sequence, but this time she took no notice and went away.

GENERAL REMARKS AND CONCLUSIONS.

Breeding Season: Previously given breeding records for *pugnax pugnax* and *pugilator* in the field are shown in Table I. The dates refer to presence of ovigerous females.

It will be seen that there are some discrepancies. From my own incomplete observations, it seems likely that at least in the New York region, *pugnax* has two breeding seasons, one in early July, and one in August, whereas *pugilator* does not come into full breeding condition until August. Table II gives dates and localities for these conclusions. Only observations made on clear, sunny days at low tide are included.

My observations concerning the migration of ovigerous females to damper localities and general habits agree with those of Pearse and Swartz and Safir, etc. Also, my general remarks (1941, 1943) in regard to display in young males, behavior of females, etc., apply equally well to these northern species.

Comparison of Displays and Their Rela-

TABLE II.

March 15-16	Atlantic City, N. J.	Both spp. in hibernation. Residents say crabs never active here before last half of May. Temp. 32°-42° Fah.
May 15	Port Jefferson, N. Y.	Both spp. at mouths of holes, completely inactive; no signs of feeding; no waving or fighting; dull colors.
June	Various localities near New York City	Oral reports say no waving.
Early July	Same as above	Oral reports say waving beginning.
July 16	Greenwich, Conn.	<i>pugnax</i> waving and fighting sporadically; majority females ovigerous.
July 23-26	Pelham Bay Pk., N. Y.	<i>pugnax</i> less active than at Greenwich; <i>pugilator</i> waving strongly, but not at peak of display activity. Few ovig. females of either species.
July 29	Staten Is., N. Y.	<i>pugnax</i> displaying only slightly.
Aug. 5-7	Port Jefferson, N. Y.	<i>pugnax</i> again displaying strongly, but no ovig. females seen. <i>pugilator</i> at peak of display activity; a few females ovig.
Sept. 24-28	Mamaroneck, N. Y.	Oral reports say <i>pugilator</i> waving.

tion to Phylogeny: Anatomically, by the criteria used in previous tropical studies (Crane, 1941, p. 165 ff.) *pugnax* and *minax* belong to Group 2, along with *mordax*, *schmitti*, *brevifrons*, etc., while *pugilator* turns out to be quite distinct from any of the six groups so far recognized, although it has affinities with Group 4 and Group 5. When the displays of these three northern species are analyzed, they are found to follow closely this anatomical placing. Previously *mordax* and *pugnax rapax* were the only Group 2 members of which I had seen the display; both are "jerkers;" that is, the wave is broken on the down or up beat or both by a series of jerks. Both northern Group 2 forms, *pugnax pugnax* and *minax*, are likewise jerkers, (although the trait is poorly developed in *pugnax*), and include in their displays other Group 2 characteristics including slowness, kicking of the ambulatories and posing motionless with outstretched appendages. Likewise, both live primarily in typical, muddy, Group 2 habitats, varying chiefly in salinity, both are relatively phlegmatic, and both are dull in color. In addition, however, the display of *pugnax pugnax* has characteristics, including the curtsy, which, compared with the southern *pugnax rapax*, appear to be of more than subspecific importance and are another sign that, in evolution, a change in behavior may precede a change in structure. It may be noted here that there are also color differences between the two subspecies, especially in the presence of bright blue eye-stalks in the northern form.

The difference in the displays of the four known Group 2 "jerkers" may be tabulated as in Table III. Differences of rhythm, and special climactic behavior are omitted.

TABLE III.

<i>mordax</i> :	Cheliped jerks on both up and down strokes.
<i>minax</i> :	Jerks on down stroke only.
<i>pugnax rapax</i> :	Jerks on way up only (when displaying strongly; otherwise both on up and down strokes).
<i>pugnax pugnax</i> :	Jerks scarcely perceptible; can be on either up or down strokes, or on both.

Of all the fiddler crabs so far studied, *pugnax pugnax* appears to have the most variable, least definite display. Even in a colony apparently in full breeding condition, there is nothing of the constant flashing of chelipeds so characteristic of many tropical forms. Instead, small waves of display run through a colony, and, as has been pointed out, the individual variation is great. The unqualified success of the species in the north is attested by the enormous colonies

found; in this region, at least, their proper habitats are far more numerous than those of the other two species, and the individuals are correspondingly more abundant. It seems possible that in this adaptable, thriving species, the display may be tending to break down, perhaps through lessening need for it as a recognition device, since the vast majority of the colonies of *pugnax* are unmixed with individuals of either of the other species. The other probable use of display—that of stimulation—may be also less necessary here, because of climatic or other influences of which we at present know nothing. The other hypothesis is also possible, that the display of *pugnax* is primitive even compared with those of other primitive Group 2 crabs; nevertheless it must be remembered that it contains the specialized curtsy element.

Uca pugilator, the sand fiddler, on the other hand, is related basically to both the Group 4 "rappers," in its display and in the form of the minor cheliped, and to the Group 5 series, (which are noted for their adaptations to relatively dry habitats and for their apparently high type of nervous organization and great activity), in its spoon-tipped hairs and in the form of its abdominal appendage. In designing a phylogenetic tree to include the Atlantic forms, at the present time I would place *pugilator* as a long offshoot near the base of the Group 4 stem, and the Venezuelan *cumulanta* from another, shorter, basal offshoot. *U. minax*, *pugnax* and *pugnax rapax* should all be placed near *mordax* and *schmitti* in Group 2. (See Crane, 1941, p. 166, text fig. 5).

Importance of Unsolved Problems: The fiddler crabs are especially worthy of detailed study because of two related facts. In the first place, they are at the summit of crustacean development in nervous organization. Secondly, in sexual dimorphism and complexity of display they rival the members of the remaining groups—all higher in the evolutionary scale—in which these characteristics reach their maximum, namely, salticid spiders, certain insects and some fishes, lizards and birds. In a comparative study of animal display, therefore, their position is fundamental.

There remain numerous unsolved problems concerning *Uca* behavior, the solutions of which are essential to a proper understanding of display. Any persons trained, or even sufficiently interested in natural history observation and experiment, could undertake some of these studies successfully, provided only that they could live close to a colony of fiddlers over a period of time. The geographical locality is of no importance. The following questions list only a few of the more obvious problems.

How do the males recognize females of

their own species? In some cases I have found that temporary, brief mistakes are made by both sexes. Is it by scent? I can find no constant, morphological sexual dimorphism in the first antennae which might indicate a higher development of the male sense of smell.

Is color vision developed in *Uca*, so that the brightening of male color in display may actually be of value in recognition and stimulation of the female? Or are the colors only by-products of endocrine activity and/or nervous excitement, of no practical value to the crab? Is brightness, as apart from color, of similar value?

What is the exact seasonal and individual development of display in each species? What is the significance of shelter-building? Of posing?

What is the use, presumably in feeding, of the spoon-tipped hairs on the merus of the second maxilliped? Why should they attain their greatest development in species inhabiting sandier localities?

What happens in the display of *pugnax* in localities, such as Key West and Havana, where the two subspecies intergrade (Rathbun, 1918, p. 398)? Through the study of details such as this, much light may be shed on the evolution of display in general.

Dembowski's (1925) observations of the "speech" and play of *Uca* should be continued.

Endocrine research in connection with the display of these crabs has yet to be started. The excellent laboratory work already done on eye-stalk hormones and their effect on color and moulting will form a useful foundation. Kleinholz (1942) gives a comprehensive survey of the work done, and includes a full bibliography.

It cannot be stressed too strongly that experiments and observations on the display of these animals must be conducted in the field, since laboratory animals do not behave naturally, either in color changes or breeding sequences. Of equal importance to the observer is the use of a large supply of patience, especially in studying the less active forms, such as those in Group 2. As has been pointed out in previous papers, the vast majority of all waving by individual crabs does not result even in attracting the attention of a female, much less does it culminate in mating. Yet it must not be decided on this account that it is of use only in demarcating territory or warning off rivals, as seems still to be the opinion of some writers. Anyone who has finally watched a pair of fiddlers in the later stages of courtship will be completely convinced of the ultimate use of waving.

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